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A NEW SUBSPECIES OF *COENONYMPHA TULLIA* (MÜLLER) (NYMPHALIDAE: SATYRINAE) CONFINED TO THE COASTAL DUNES OF NORTHERN CALIFORNIA

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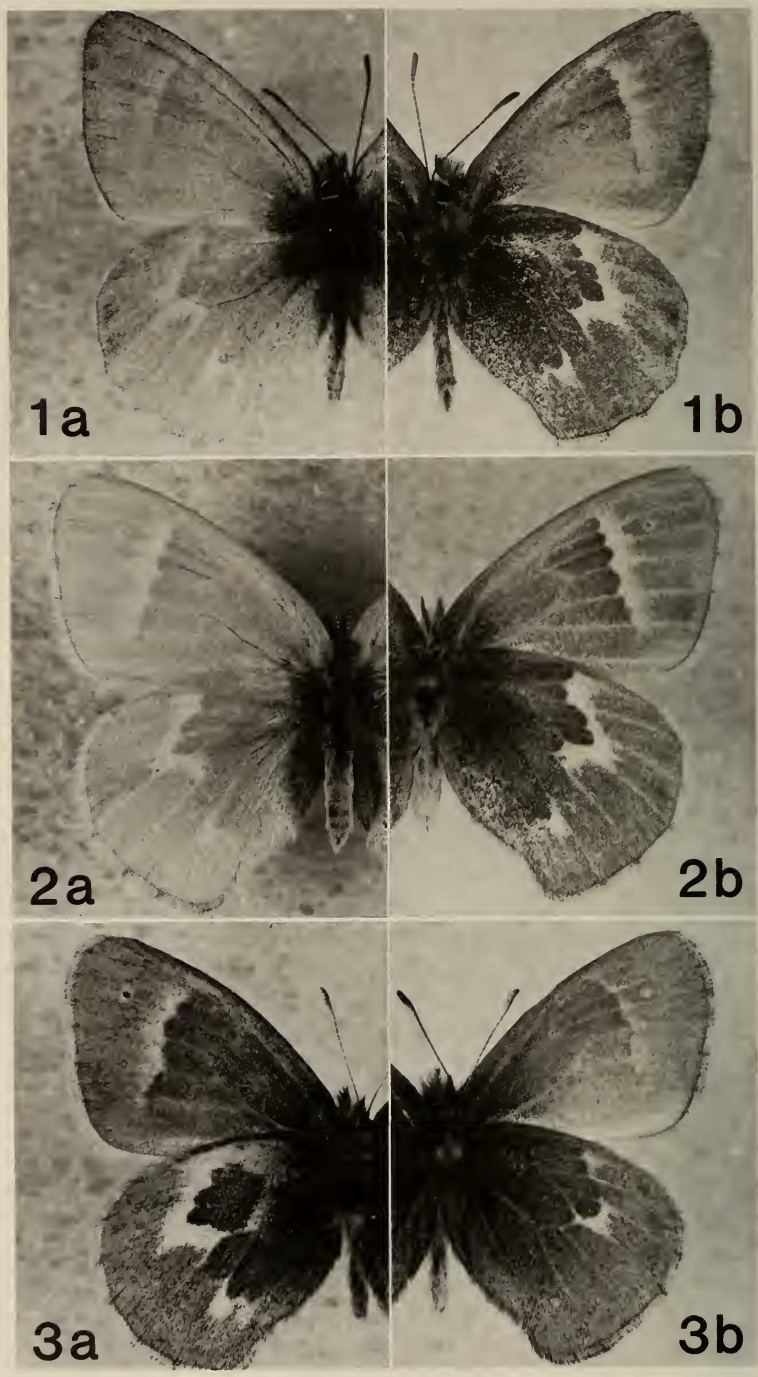
ABSTRACT. *Coenonympha tullia yontocket* is described from a single known population confined to the coastal sand dunes north of Crescent City, Del Norte County, California. It is most similar in phenotype to *C. tullia eunomia* Dornfield, but may be distinguished by wing characters. A population of *C. tullia eryngii* Hy. Edwards occurs ten kilometers away; these two populations show no clear signs of reciprocal introgression in wing characters. Electrophoretic analysis indicates that *yontocket* retains the high genetic variability characteristic of other *tullia*-group taxa, but no diagnostic alleles were found. The high genetic variability is most likely maintained by gene flow from *eryngii*. *Coenonympha tullia* subspecies *yontocket, eunomia, eryngii,* and *california* Westwood are genetically very similar (Nei's unbiased genetic distance <0.035). The data justify the placement of *yontocket* as a subspecies rather than a species. This subspecies is a likely candidate for listing as threatened in California; collectors and developers are urged to protect this population from extinction.

Additional key words: *Coenonympha tullia yontocket,* taxonomy, electrophoresis, ringlets, threatened species.

Investigation of the coastal dunes of northern California has turned up a unique population of the widespread Ringlet butterfly, *Coenonympha tullia* (Müller). This population occurs in the vicinity of Crescent City, Del Norte Co., and has an ochre ground color; it is wholly contained within the range of *C. tullia eryngii* Hy. Edwards, a widespread subspecies with a whitish ground color. It is quite similar phenotypically to *C. tullia eunomia* described by Dornfield (1967), whose nearest known population is 250 km away in the Umpqua River drainage in southeastern Oregon (Porter & Geiger 1988). This new population flies in the fog belt, and shows the heavy melanization of the wings and body characteristic of butterflies from this type of environment (Hovanitz 1941, McCorkle & Hammond 1988).

Herein, we provide a description of this population as a new subspecies, and justify our taxonomic placement with genetic evidence from electrophoretic analysis. We did not examine genitalic or larval characters: Davenport (1941) indicated that all *tullia*-group taxa were indistinguishable genitalically despite high levels of intrataxon variability, and description of the immature stages would be of little taxonomic use given our small series and the lack of comparative material.


1a
1b
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Coenonympha tullia yontocket, new subspecies
(Figs. 1–3)

Description. Holotype (Fig. 1): male; dorsal ground color dull ochraceous; medium to light gray scaling along the costal and distal forewing margins, extending proximally along the veins. Dorsal hindwing with gray scaling along distal margins, stronger in anal area. Eyespots absent; ventral whitish markings barely visible from above. Both dorsal surfaces strongly melanized subbasally. Ventral forewing ground color deep ochraceous, almost orange; medium band whitish, extending from R veins to Cu_2; ground color fades to whitish, then greenish gray in costal and apical regions, becoming strongly suffused with melanized scales; eyespots absent. Ventral hindwing ground color brownish ochre in discal region, fading to greenish gray beyond the median markings. Median band whitish, well marked; absent only between Cu_1 and Cu_2. Whitish basal patch present at radial vein. Eyespots absent. Darkened, single marginal line on all wing surfaces, well expressed ventrally. Head, thorax, and ventral hindwing bases covered with long hairs matching ventral hindwing ground color.

Morphological variation (Figs. 2, 3). Forewing length, males: 14–18 mm (n = 65); females: 15–19 mm (n = 10). Spring brood averages slightly larger (males: $\bar{x}$ = 16.3 mm; n = 52) than fall brood (males: $\bar{x}$ = 14.7 mm; n = 17). Spring brood: gray scaling dorsally along the distal margins of both wings may be almost absent, but may extend proximally in extreme individuals (n = 2) so that the outer third of the wing is pale gray. Ventral forewing median band whitish; extends from R veins to Cu_1 or Cu_2. Single ventral forewing eyespot absent in most individuals, but may be up to 1 mm diameter, unpupilled ochraceous or yellow, or yellow pupilled with black. Ventral hindwing: ground color sometimes obliterated by melanized scaling in discal area; wholly brownish or wholly greenish in some individuals. Median band sometimes weakly expressed between Cu_1 and Cu_2, rarely absent below M_3 (Fig. 3b). Whitish basal patches often present, connecting to median markings via the costa in extreme individuals (n = 2) (Fig. 3a). Eyespots absent in almost all individuals; rarely up to three, yellow or yellow with black pupils, most likely between Cu_1 and Cu_2. Marginal line often double. Females (Fig. 2) tend towards less melanization, broader wings. Fall brood: markings similar to spring brood, more animals with brownish rather than greenish ventral ground color, and more likely expression of ventral basal patches.

Diagnosis. Separable immediately from nearby populations of *eryngii* by the ochraceous ground color. Separable from *eunomia* ventrally by stronger expression of the medial markings; from *eunomia* and *ampelos* ventrally by the frequent occurrence of basal patches, and dorsally by gray scaling along the veins and outer wing edges.

Distribution. Known only from Del Norte Co., California, among the coastal sand dunes north of Crescent City, beginning at the north shore of Lake Earl and extending north 7.5 km to the south bank of the Smith River (Fig. 4). This area is hereby designated as the type locality. Seemingly suitable habitat between Lake Earl and Point St. George may also be populated by *yontocket*. Not present in abutting disturbed habitats to the east (mostly cow pastures), or at the dunes north of Arcata Bay in Humboldt County, California. Replaced by *eryngii* 10 km to the east on exposed serpentine hilltops.

Material examined. Holotype: Male, California, Del Norte Co., 4 km W Fort Dick, 8-IX-1979, leg. S. O. & E. Mattoon. Deposited in the Bohart Museum at the University of California, Davis. Paratypes: California, Del Norte Co., 4 km W Fort Dick, end of Kellogg Rd. S to north shore of Lake Earl, 2-VI-1979 (15 males), 30-VI-1979 (4 males) & 8-IX-

←

FIGS. 1–3. **1,** *Coenonympha tullia yontocket* holotype male; (a) dorsal and (b) ventral surfaces. **2,** *Coenonympha tullia yontocket* paratype female; (a) dorsal and (b) ventral surfaces. Unlike this specimen, many females do show basal ventral hindwing patches. **3,** *Coenonympha tullia yontocket* ventral surfaces, showing the extremes of expression of maculation. The reduced pattern of (b) is characteristic of *C. tullia eunomia* populations.

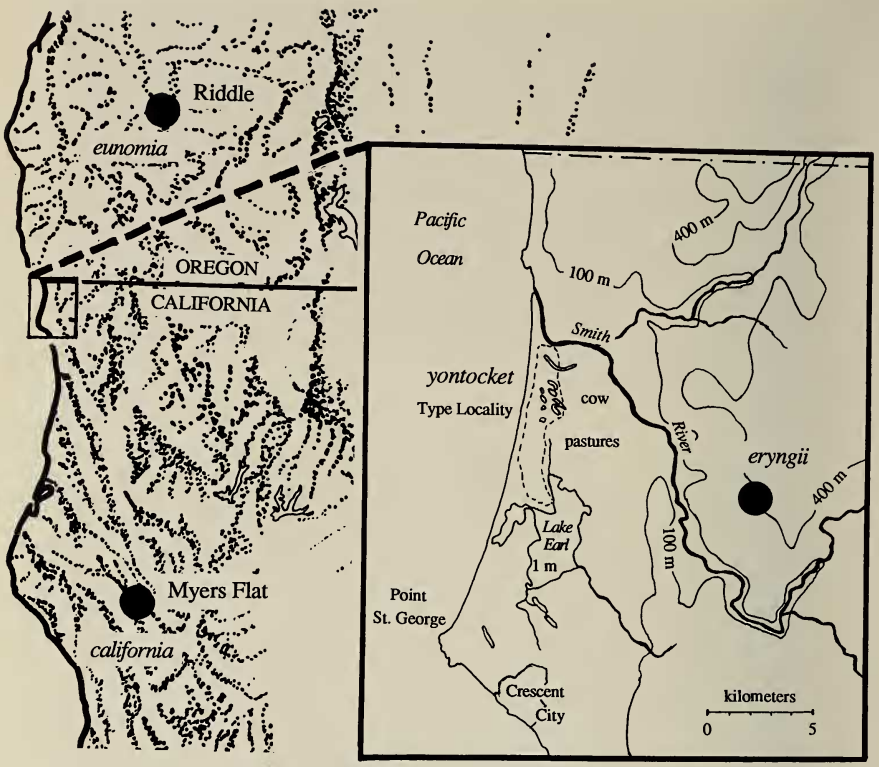

FIG. 4. Map showing localities sampled in northwestern California and southwestern Oregon. Note the close proximity of the *eryngii* population to the type locality of *yontocket* (inset). Neither subspecies occurs in the intervening cow pastures.

1979 (16 males, 2 females), S. O. & E. Mattoon, leg. These will be deposited in the Bohart Museum, the California Department of Food and Agriculture, the California Academy of Sciences, the Los Angeles County Museum, the Allyn Museum, and the National Museum of Natural History, Smithsonian Institution. Additional material: wing vouchers from specimens used for electrophoretic analysis (29 males, 8 females), collected from the Yontocket Archeological Site at the north end of the population range.

Biology. Flight periods May–July and September-October. Habitat: elev. 2 m; in grassy areas among dunes with coniferous lee slopes and grassy exposed slopes, and among dunes on slightly elevated ground around seasonally marshy sphagnum bogs which fill during the rainy season. 2 females oviposited (5 observations) on dry grass stems (mixed species composition) approx. 2–5 cm above soil in areas free from flooding. Larvae and pupa (n = 2 larvae; 1 pupated) are apparently not different from those of *eryngii* (n = 8 larvae; 2 pupated). Larval host(s) presently unknown.

Etymology. *Coenonympha tullia* subspecies are often given American Indian names. This population is dedicated to the memory of the Yontocket tribe, which once had seasonal settlements in these dunes.

In deciding to name this population, we considered two points: (i) is it sufficiently distinct from *C. t. eunomia* to warrant taxonomic recognition?, and (ii) given that an apparently permanent population of

C. t. eryngii occurs in serpentine grassland habitat on a hilltop 10 km to the east and within sight of the *yontocket* population (Fig. 4), should *yontocket* be given species status? To address these questions, we performed starch gel electrophoresis to provide insights into the genetic relationships among the *yontocket* population, the nearby *eryngii* population, a previously studied *eunomia* population from Riddle, Oregon, and a *C. t. california* Westwood population from near Myers Flat, Humboldt Co., California. Each of these populations comes from relatively isolated areas of grassland habitat, providing a control on the potential for genetic differentiation resulting solely from variation in local population structure. Previous work has established that *eryngii, california,* and *eunomia* are members of a single polytypic species (Porter & Geiger 1988).

MATERIALS AND METHODS

Butterflies were netted and temporarily stored on wet ice, hand-carried or mailed back to Davis, then frozen alive at −80°C for storage until analysis. Electrophoretic analysis followed the protocol of Ayala et al. (1972) and Geiger and Shapiro (1986), with one modification: rather than using sponge wicks to complete the circuit between the electrode buffer solutions and the gels, gel molds were used which allowed the ends of the gels to contact the electrode buffer directly. We scored 13 loci: adenylate kinase (AK-1), aldolase (ALDO), fumarase (FUM), glutamic-oxaloacetic transaminase (GOT-1, GOT-2), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), α-glycerophosphate dehydrogenase (α-GPDH), isocitrate dehydrogenase (IDH-1), malate dehydrogenase (MDH-1, MDH-2), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI), and superoxide dismutase (SOD-1). Zymograms were scored as described in Porter and Geiger (1988), and data were analyzed using the computer program BIOSYS-1 (Swofford & Selander 1981).

RESULTS

Allelic frequencies for the *yontocket, eryngii,* and *california* populations are given in Table 1; allelic frequencies at these loci were previously given for the *eunomia* population in Porter and Geiger (1988). All populations show high levels of genetic variability. characteristic of *Coenonympha tullia* populations elsewhere (Table 2; Porter & Geiger 1988); this is an indication that the *yontocket* population has not been through a significant genetic bottleneck in its recent past. Table 3 shows genetic relationships among these populations using Nei's unbiased minimum distance and identity measures (Nei 1978). The phenogram constructed based on these values using UPGMA (Fig. 5; see Sneath &

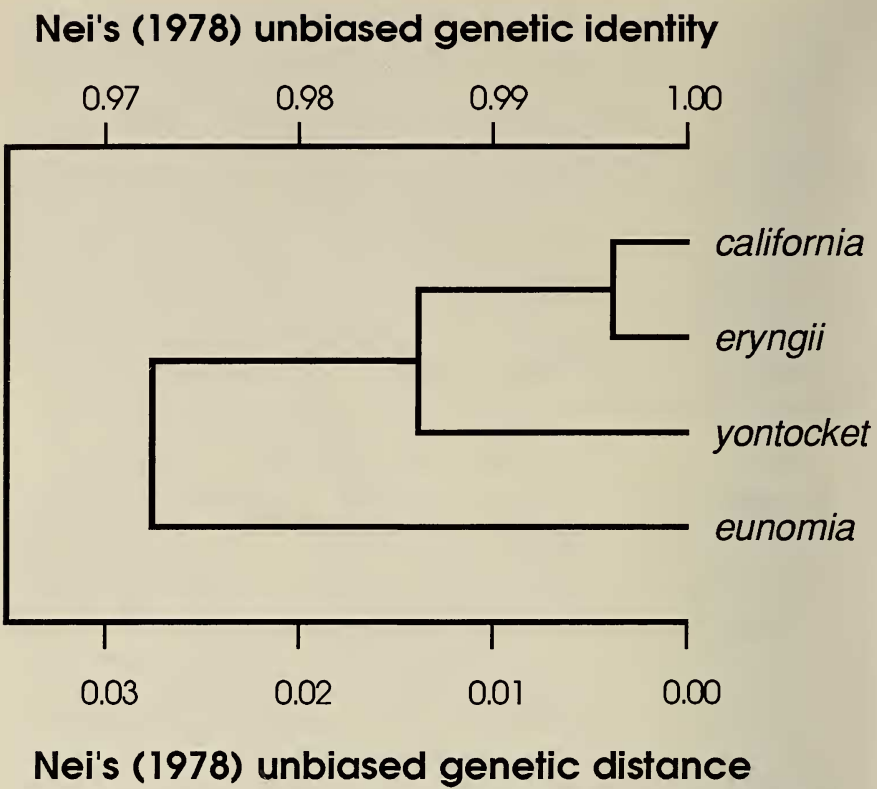

FIG. 5. Phenogram of genetic relationships constructed using the UPGMA algorithm on data from Table 3. *Yontocket* does not cluster with *eunomia*, but all populations are genetically very similar.

Sokal 1973 for methodological details) does not group *yontocket* with *eunomia*, despite their general similarity in wing characteristics. These distance-identity values indicate a very low level of genetic differentiation overall, corresponding to subspecies-level differentiation in most taxa (Thorpe 1983), including butterflies (AHP unpubl. data; H. J. Geiger, pers. comm.).

DISCUSSION

Neither the *yontocket* nor *eryngii* population in Fig. 4 has colonized intervening, non-native grassland presently used for grazing. There is also no clear evidence of introgression in wing pattern traits in the animals we sampled. The pale gray along the veins and wing edges dorsally in *yontocket* may well be evidence of such introgression, but populations from the Pit River drainage in eastern California, where

TABLE 1. Allelic frequencies of *Coenonympha tullia*-group taxa. Population localities and locus abbreviations given in the text.

Locus and allele	Taxon			Locus and allele	Taxon		
	california[1]	*eryngii*[2]	*yontocket*[3]		*california*[1]	*eryngii*[2]	*yontocket*[3]
AK-1				MDH-1			
76	0.056			91	0.028	0.014	
86			0.023	93	0.028		
90	0.361	0.275	0.500	100	0.861	0.986	0.932
100	0.556	0.675	0.432	105	0.028		
102	0.028			110	0.056		0.068
110		0.050	0.045	MDH-2			
ALDO				96	0.028		
100	1.000	1.000	1.000	100	0.972	0.917	0.932
FUM				105		0.069	0.054
100	1.000	1.000	1.000	110		0.014	0.014
GAPDH				PGI			
100	1.000	1.000	1.000	81			0.014
GOT-1				88	0.028		0.014
89	0.028	0.014		94		0.028	
91	0.194	0.111	0.135	97	0.083		
94			0.041	100	0.306	0.333	0.284
100	0.778	0.806	0.730	103	0.056	0.028	
102		0.056		107	0.306	0.389	0.662
108		0.014	0.054	105		0.042	
110			0.041	111	0.028	0.069	
GOT-2				114	0.194	0.056	0.027
100	0.944	0.944	0.973	117		0.014	
112	0.056	0.056	0.027	121		0.042	
α-GPDH				PGM			
75	0.028			90		0.014	
90		0.042		94	0.028	0.042	
96		0.014		97		0.028	0.027
100	0.972	0.931	1.000	100	0.361	0.486	0.662
110		0.014		106	0.528	0.389	0.311
IDH-1				110	0.083	0.028	
90	0.028	0.014		112		0.014	
92	0.028	0.028		SOD-1			
100	0.417	0.583	0.730	89	0.028		
103	0.194	0.208	0.108	100	0.944	1.000	1.000
106	0.306	0.125	0.162	120	0.028		
111	0.028	0.042					

[1] n = 18.
[2] n = 36, except at AK-1, where n = 20.
[3] n = 37, except at AK-1, where n = 22.

california and *eryngii* (white ground color), and *ampelos* (ochre ground color) intergrade, produce many specimens of wholly intermediate background coloration (Porter & Geiger 1988). These observations suggest that differentiation is maintained by behaviors related to habitat and(or) host-plant selection—but not necessarily by reproductive barriers.

Phenograms based on genetic distance-identity indices are often used

TABLE 2. Genetic variability statistics for the three populations given in Table 1. Mean number of alleles per locus = $\bar{x}_{alleles}$. Percent of loci polymorphic = P. Observed heterozygosity = H_{obs}. Heterozygosity calculated from Hardy-Weinberg proportions = H_{exp}. Standard errors in parentheses.

Population	$\bar{x}_{alleles}$	P	H_{obs}	H_{exp}
california	3.2 (0.5)	84.6	0.303 (0.090)	0.283 (0.080)
eryngii	3.5 (0.7)	69.2	0.240 (0.078)	0.246 (0.076)
yontocket	2.5 (0.4)	61.5	0.199 (0.070)	0.210 (0.064)

to approximate phylogenetic relationships between species, but these measures can only reflect overall genetic differentiation within a species. Within a species, the degree of differentiation expressed among populations reflects a balance between the forces of natural selection, genetic drift, mutation, and gene flow acting at each locus. The fact that *yontocket* is more similar to *california* and *eryngii* than to *eunomia* implies that gene flow between *yontocket* and *eunomia* is interrupted: it seems unreasonable to consider them consubspecific. This interpretation is also in agreement with the disjunct distribution of these taxa.

The high level of variability in *yontocket* enzyme characters also requires explanation. The *yontocket* population probably has an effective breeding population of moderate size, and is likely to be affected somewhat strongly by genetic drift. If *yontocket* is fully reproductively isolated from *eryngii*, then *exceedingly* strong selection on these enzymes is required to maintain such high numbers of alleles; on the other hand, infrequent influxes of *eryngii* phenotypes could easily maintain this variability. Given that there is evidence of some gene flow between *eunomia* and *eryngii* in southeastern Oregon (Porter & Geiger 1988) (the subspecies separated by the greatest geographic distances in the phenogram of Fig. 5), and that *yontocket* is of intermediate similarity, we think it is wise to place *yontocket* as a subspecies of *tullia* unless subsequent studies on reproductive biology demonstrate intrinsic barriers to gene flow. The level of current gene flow between these two adjacent *tullia*-group populations, based on their present constellations of allelic frequencies, indicates that these populations exchange between four and five breeding individuals every generation on average (Porter, in prep.), further supporting the taxonomic placement proposed here.

The evolutionary origins of the diagnostic *yontocket* traits are explainable by a number of plausible scenarios (many non-diagnostic traits may be attributable to gene flow from *eryngii*). The most likely scenario is that these traits arose from *eunomia* or even *columbiana* McDunnough, which may have had more southerly distributions during the last glacial stages. A population of *Polites mardon* (Edwards) (Hesperiidae) also occurs in Del Norte Co., California, disjunct from nearest

TABLE 3. Nei's (1978) unbiased genetic identity (above diagonal) and distance (below diagonal) values between population pairs. Populations given in the text.

Taxon	Taxon			
	california	*eryngii*	*eunomia*	*yontocket*
california		0.997	0.976	0.982
eryngii	0.003		0.974	0.990
eunomia	0.030	0.035		0.979
yontocket	0.018	0.010	0.026	

known populations in southwestern Washington State (Scott 1986; T. C. Emmel, J. F. Emmel & S. O. Mattoon, in prep.). However, this alone does not explain the high incidence of the basal ventral hindwing patches, a characteristic of populations in the Great Basin and Rocky Mountains. Whether the basal ventral patch is adaptive, ancestral in North America, or exists in *yontocket* as a result of past gene flow from the east, is unknown. Functionally unrelated traits can clearly have independent geographic ranges within a species. Thus, the conclusions we draw concerning the historical biogeography of *tullia*-group traits depend largely on whether or not biological species boundaries exist within the complex (and if they do exist, where they are).

We think it is particularly important to recognize the threat of extinction to *C. t. yontocket* caused by habitat destruction. The southern end of the population distribution occurs in habitat patches within an abandoned gridwork of streets originally intended as a housing development. With the spread of development by the tourist industry around the recently formed Redwood National Park, the *yontocket* habitat is likely to become attractive to developers of beachfront property—both for private and public use. Given the failure of *yontocket* to invade adjacent cow pastures, a habitat used by *tullia* subspecies elsewhere in western North America, it is likely that such development will have severe impact on this population. We urge lepidopterists to refrain from collecting in this fragile ecosystem, and to provide support for groups dedicated to the preservation of this and other threatened taxa along the Pacific Coast.

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